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ON THE MOUTH-PARTS OF THE HEMIPTERA.

BY WALTER J. MEEK.

With plates VII, VIII, IX, X, and XI.

THE general structure of the hemipterous mouth was known to Savigny, but only in recent years has detailed work on the subject been attempted. In 1883 Otto Geise* presented a paper on the mouth-parts of some Hydrocorisæ, and in 1885 Herman Wedde published a similar one on the Geocorisæ. Two years later Leon studied the mouth of *Pentatoma*. In 1902 Smith advanced an explanation for the morphology of the hemipterous mouth, and later these views were commented upon by Marlatt. Heymons, in 1899, wrote on the morphological history of the Hemiptera.

Geise in his work discusses and illustrates clearly the mouth-parts of *Notonecta glauca*, *Nepa cinerea*, and *Corixa striata*. He advances nothing new as to the morphology of the parts. The pharynx or "Schlundkopf" and the "Wanzenspritze," which we shall term the salivary injector, are carefully discussed. The pharynx is composed of the well-developed epipharyngeal and hypopharyngeal lamellæ. The latter is greatly modified, having many cutting and grinding processes, evidently used in preparing the food. The muscles that raise the epipharynx are arranged in groups. The structure of the injector is more nearly constant in the three forms than that of any other organ.

For his investigations Wedde selected *Pyrrocoris apterus*. He describes the pharynx as being a simple unmodified tube. It is supported and fastened to the head walls by a complicated

* For this and the following references, see bibliography at the end of this article.

chitinous structure, which Geise does not find in his specimens. The injector is very much the same as described by Geise.

Leon uses *Pentatoma* as the subject of his investigations, and, in a great measure, reproduces the work of Geise. The most interesting part of his paper is his discussion of the morphology. He considers the maxillary palpus as having disappeared with the maxilla's change of function. On one of the Tingitidæ from Ceylon he finds vestigial three-segmented labial palpi. He presents this fact as an argument for the belief that the labial palpi are lost in the Hemiptera, and that the labium is, therefore, composed of the submentum, mentum and glossæ and paraglossæ fused to form the terminal segments.

The *Cicada* nymph was used by Smith in his investigations. His explanation of the mouth-parts is, in brief, the following: The anterior sclerite on the cephalic aspect of the head is the labrum. Just behind the labrum is the mandibular sclerite, which is the true mandible. The maxilla is represented by the two stylets arising from one base, to which is attached the vestigial maxillary palpus, and by the sheath, usually recognized as the labium. The bristles represent the lacinia and the stipes of the maxilla, according to his work. The development has been the same as in the case of the Diptera. The basal joint of the beak is the cardo, the second segment the subgalea, and the third and fourth the two joints of the galea. All that remains of the labium is the mentum, a boat-shaped process lying between the stylets.

Smith's homologies seem to be fanciful. He apparently felt determined to make the changes in the mouth-parts correspond to those already found in the Diptera. In his dissections he seems to have overlooked the fact that the stylets do not arise from one base. Had he observed this, it would have been evident to him that his theory would not hold good. The boat-shaped process which he names the mentum will be recognized as the pharynx. Smith's paper has been severely criticized by Marlatt. Marlatt gives Smith well-deserved credit for calling attention to the mandibular and maxillary sclerites, but at the same time he refuses to accept the explanation of the morphologies.

The morphological development of the Hemiptera has been investigated by Heymons (1899). It is gratifying to know that

the morphologies advanced by him agree in the main with those held by earlier investigators.

It will be seen that, in Hemiptera, the Heteroptera have been the subject of most frequent investigation. The Germans, who have done by far the best work along this line, used these forms almost exclusively. For this reason the suborder Homoptera has been selected, and the purpose of this paper will be to give the detailed structure of the homopterous mouth as shown in one of the Cicadidæ and to compare it with the buccal structures of the Heteroptera.

The seventeen-year locust, *Cicada septemdecim*, on account of its large size and its abundance at certain periods, has been chosen as the type for study. The specimens were collected during their last appearance in this vicinity, May, 1895, by L. L. Dyche, at Lakeview, and by R. G. Gowell, at Linwood. This material was thrown into 95 per cent. alcohol, where it has since remained. The cicadas have been well preserved for anatomical study, especially the chitinous and muscular structures.

TECHNIQUE.

In order to study the structure of the head, coarse dissections were first made with the needle and knife, and then finer ones with the microtome. The first method, of course, needs no explanation, only it may be remarked here that it is an exceedingly valuable way to work out the orientation of the parts.

Great care is necessary in preparing specimens for the microtome, and also in staining and mounting the sections. The hard, brittle chitin makes it impossible to secure sections without first softening the chitinous parts. This may be accomplished by soaking the head from ten to twelve hours in a solution of Eau de Labarraque, consisting of one part Labarraque to six parts water. With a solution of this strength the muscular structure will be very slightly injured, if at all. From the Labarraque carry the specimen through various grades up into 95 per cent. alcohol.

For embedding, celloidin-paraffin methods have been used. Celloidin of any desired strength may be made by dissolving the well-dried celloidin in equal parts of ether and absolute alcohol. After the specimens have been properly dehydrated they were removed to the 4-per-cent. celloidin solution. *Cicada* heads were left for at least ten days or even longer.

Some satisfactory slides have been made from heads which remained in celloidin for three months. Instead of transferring the specimens to thicker solutions, it is easier and just as well to let the 4-per-cent. solution gradually thicken by evaporation. When the celloidin has reached a jelly-like consistency, the heads were removed and hardened in chloroform. On entering the chloroform the celloidin will usually turn opaque, but this condition disappears as the hardening process is completed. When the specimens are hardened, usually from one to several hours, they may be placed in the paraffin bath, and in another hour they are ready to be molded into blocks of paraffin. The specimens may now be kept indefinitely.

The above method is entirely satisfactory, but it is long and cumbrous. The Gilson process described by Lee is much more expeditious. The object is dehydrated, soaked in ether, and put in a test-tube with a thin solution of celloidin. The tube is then dipped into the paraffin bath and the solution boiled down to about one-third of its volume. The mass is then turned out and hardened for several hours in a mixture of equal parts of chloroform and cedar-wood oil. The specimens may now be molded into blocks of paraffin as before. The best results are obtained by dry cutting.

For staining, Delafield's hæmatoxylin and picric acid have been found most useful. The hæmatoxylin is a good nuclear stain, while the picric acid is a valuable secondary stain for distinguishing chitin. In staining, the usual method of procedure is followed. The sections may be cleared in cedar-wood oil or other clearer and mounted in balsam.

NOMENCLATURE.

The nomenclature of the insect head has been based on anatomical work entirely, and for that reason it has little morphological value. Some of the primitive sclerites are indistinct, while others have developed greatly. The result is that a given named area may include several sclerites or perhaps only a portion of one. This nomenclature, however, is sufficient for the description of parts, and when supplemented with explanations it will serve for morphological work. All terms denoting location of parts are used with the head in the feeding position. The beak is then at right angles to the body line.

EXTERNAL AREAS OF THE HEAD.

The general appearance of the *Cicada* head is familiar to most students. It is an isosceles triangle in shape. The vertex of the head marks the base, and at the basal angles are the large compound eyes. From the lower angle extends the slender, three-jointed beak or proboscis. From the cephalic aspect, the most prominent part of the head is the swollen, deeply furrowed frons. Beneath it is the smaller, roof-like clypeus. Laterad of both frons and clypeus lie the crescent-shaped loræ or mandibular sclerites. Still laterad of these lie the narrow maxillary sclerites. From the vertex to the tip of the beak the head averages 10 mm. in length, and from eye to eye it averages 7.5 mm.

THE EPICRANIUM.—(Fig. 1, *e*.) In generalized insects the dorsal surface of the head is marked by a well-defined Y-shaped epicranial suture. The sclerites lying back of the arms of the letter and adjoining the stem form an area known as the epicranium. Such an area (fig. 1, *e*) is easily observed in the *Cicada*, but the suture is T-shaped. The cephalic part of the epicranium is called the vertex, and this bears the three ocelli.

THE FRONS.—(Fig. 1, *f*.) Between the epicranial suture and the beak are three sclerites. The first of these and also the largest, a convex shield in shape, occupies the middle part of the cephalic aspect of the head, and is named the frons. The sclerite is protruding, with a deep wrinkle or fold along the median line. On each side, running laterad, are series of furrows, usually eight in number. The lower edge of the frons is narrower than the upper, and the junction with the clypeus is made in a curved line.

THE CLYPEUS. (Fig. 1, *c*.) The clypeus is the intermediate of the three cephalic sclerites. It resembles the frons in shape, but is considerably smaller in size. The elevation along the median line continues as in the sclerite above. The deep median sulcus, however, which is so characteristic of the frons, is not present.

THE MANDIBULAR SCLERITES. (Fig. 1, *mds*.) These have already been mentioned as lying laterad of both the frons and clypeus. They are crescent-shaped, sparsely covered with long hair, and are closely applied to the sides of the head. Dorsad

they meet the genæ. Their outer margins meet the maxillary sclerites, and their mesal sides are bounded by the frons and clypeus. The sclerite extends downward for half the length of the clypeus.

THE MAXILLARY SCLERITES. (Fig. 1, *mxs.*) Laterad of the mandibular sclerites are the long, narrow chitinized strips forming the lower lateral edges of the head. These are the maxillary sclerites. Viewed caudad they are much wider and lighter in color. They form the boundary for the lower part of the occipital foramen. The lower part projects into a mesal pointed piece, the maxillary process (fig. 4, *procx*), which in the normal position covers the hypopharynx and is closely appressed to the stylets.

MOUTH-PARTS. Before proceeding to descriptions of the individual organs, it may be well to note the main features of the insect mouth and the modifications they have undergone in the orders of sucking insects. The mandibulate mouth consists of two pairs of laterally working, shear-like jaws, covered above by the labrum and closed below by the lower lip, the labium. The inner surface of the labrum is sometimes developed into the epipharynx. The labium also bears on its inner surface a well-developed ligula or hypopharynx.

In the suctorial mouth the four jaws have elongated and become setiform. The labrum has been greatly reduced and the labium has become a canal-shaped beak inclosing the setæ. These homologies were long ago determined by anatomists. Westwood says of the Hemiptera: "The mouth is of the promuscid construction, the labium or canal being occasionally greatly elongated and extending beneath the body, and is either three- or four-jointed. The four internal delicate setæ represent the mandibles and the maxillæ." It is very gratifying to know that recent embryological work is verifying these early homologies.

THE LABIUM. (Figs. 1 and 2.) The most prominent of the *Cicada* mouth-parts is the labium. Early investigators termed the organ haustellum, rostrum, promuscis, proboscis, Schnabel, or Rüssel, but in late years, since more attention has been given to homologies, the name labium has come into favor and it will doubtless remain. The labium, then, the most noticeable part of the suctorial mouth, projects from the lower angle of the

head, and when at rest lies between the coxæ of the thoracic legs. In cross-section it is elliptical in shape. Its entire length is about 5¾ mm. In many Hemiptera this beak is divided into four segments, but in the *Cicada* there are only three. Of these the distal segment, the longest, averages 3¼ mm.; the middle one, 1 mm.; and the proximal, 1¼ mm. Since each segment must bear muscles to move the ensuing segment, the first and second are larger in diameter than the third. The enlargement is on the lower side and the cephalic line continues unbroken to the tip.

A heavy membrane (fig. 2, *m*) attaches the labium to a chitinized collar of the thorax. It should be noticed that the labium seems to belong to the thorax rather than to the head. In separating the head from the body, the beak is frequently left behind, because the attachment there is stronger than that binding it to the head. In the same manner, but by a more delicate membrane, the labium is fastened to the hypopharynx, or, speaking more accurately, the hypopharynx, an outgrowth of the labial floor, is connected with the labium by a thin membrane. (Figs. 3, 4, and 14, *m*.)

The cephalic surface of the labium is folded inward longitudinally, so as to form a well-defined groove or canal. This incurved structure may be readily understood by referring to a cross-section (fig. 8). The edges of this canal are, at the basal segments, rather widely separated, but they gradually approach, and at the beginning of the distal segment they touch, forming a nearly perfect tube. From the proximal segment, the heavily chitinized floor of the canal differentiates from the connective membrane and extends upward as a free chitinized rod (fig. 2, *cr*) To this are attached the retractor and protractor muscles.

In the first segment and the proximal half of the second, the space between the edges of the labial canal is occupied by the epipharynx. The two organs are dovetailed tightly together. The outer surface of the epipharynx and the inner surface of the labial canal are both grooved, and fit into each other as shown in figure 9. This arrangement converts the canal at this point into a perfect tube. The epipharynx is flexible, and envelops the stylets, fitting closely around the maxillæ, and almost making an inner tube.

Fine hairs cover the surface of the labium and these increase

in size until at the tip they become stiff bristles. The distal segment is most strongly chitinized and the tip is blunt rather than acute. As in other forms, the lower side of the beak is marked along its median longitudinal line by a seam which is usually taken as evidence of a fusion of two maxillæ to form the one organ.

THE LABRUM. (Fig. 1.) In the *Cicada* the labrum is rudimentary. It may be seen as a minute triangular process, the apex projecting from the front margin of the clypeus into the opening made by the edges of the labial canal in the first segment. On dissection it is found to be about 3 mm. in length, with its under surface grooved and closely fitted to the underlying epipharnyx. With the change in the manner of securing food, the labrum of course became functionless. The only duty it could perform was to hold the stylets in place, but for this the epipharnyx has become much better fitted. The result has been as one would expect: the labrum is greatly reduced and the epipharynx has become comparatively much more important.

THE EPIPHARYNX. (Fig. 7, *ep*.) This organ has necessarily been described in discussing the labrum. In the *Cicada* the epipharynx resembles the labrum and has usually been confounded with the latter by investigators. It originates from the lower inner lining of the clypeus, is canal-shaped, cross sections giving a crescent (fig. 9, *ep*) and projects farther forward than the labrum. It will be referred to more explicitly when the stylets are discussed.

CAUDAL VIEWS OF THE HEAD. (Figs. 3, 4, and 5.) Before proceeding farther in the study of any one organ of the mouth, it will be well carefully to examine the head from the caudal aspect. By removing the head from the body and then the labium from the head, figure 3 may be obtained. On the vertex two large muscles (fig. 3, *ml*), which fasten at one end just within the occipital foramen and at the other to the prothorax, are prominent. Below them is the head cavity filled with glands which cannot be studied here. Extending from one side to the other across the middle portion of the head is a thin chitinous band, the tentorium (fig. 3, *t*). The median portion is slightly thickened, and this is the tentorium proper. The tendonous strands connecting the median portion with the head wall are

the posterior arms, while those (fig. 3, *at*) which sink deep into the head are the anterior. The latter may be traced to the cephalic side of the head along the line where the mandibular sclerite and the frons meet.

Connecting with the head wall, at about the same place as the posterior arms of the tentorium, are the S-shaped cervical sclerites (fig. 3, *csc*). To these are attached a complex series of muscles (fig. 3, *cm*) which fasten in the prothorax. These sclerites, figured only on one side of the illustration, may be seen in the neck of the living specimen. They serve as fulcrums on which the head is turned.

Below the tentorium and converging toward the ventral median part of the head are two large, prominent muscles (fig. 3, *min*). These form perhaps the most noticeable part of the caudal aspect. Between them is a small duct which divides into two branches (fig. 3, *sd*). From chitinous plates lying at either side of these large muscles, and forming part of the head wall, spring other large muscles (fig. 3, *mr*) which give the head its rotary motion. At their ventral ends the converging muscles just mentioned pass under a funnel-shaped, thinly chitinized structure, the hypopharynx (fig. 3, *h*). This organ is an outgrowth of the inner surface of the labium, and its connection with the latter may be easily noticed at *m*, figures 3 and 4.

On the removal of the labium, stylets are found to be concealed in the labial canal. These at first tightly adhere to each other, but they may be separated. They are then four in number. The inner pair are the smaller and more difficult to separate. The stylets diverge at the tip of the hypopharynx and are lost to sight in the head itself.

Figure 4 is a caudal view, similar to the preceding, except that the muscles and flesh have all been removed. Two thin chitinous plates (fig. 4, *cp*) support the large, converging muscles. At their dorsal end these plates are united with the posterior arms of the tentorium, and the two structures are then both attached to the head wall. At their ventral ends the plates pass without interruption into the walls of the hypopharynx. Laterad of these plates are the caudal surfaces of the head wall which support the retractor muscles of the labium (fig. 4, *cmx*), as well as the rotary muscles of the head.

Occupying the median portion of the head, and running in a longitudinal direction, is the keel-shaped and strongly chitinized pharynx (fig. 4, *p*). Its ventral end curves upward into the head and disappears behind the hypopharynx; its dorsal end becomes less strongly chitinized and gradually assumes the character of the ordinary esophagus.

Closely appressed to the hypopharynx are the distal ends of the maxillary sclerites. These are shown slightly removed in the illustrations, but normally they lie close together, their edges meeting along the median line. Their inner edges are produced into palpus-like appendages (fig. 4, *procx*), termed the maxillary processes.

MANDIBLES AND MAXILLÆ.

When the labium was removed from the head several stylets were found in the labial canal, and these we are now ready to trace out. By taking away the chitinous plates and pulling the maxillary sclerite aside, a view will be obtained corresponding to the right half of figure 5.

The setæ first exposed to view are the smaller, inner ones, and from their caudal position we know that they are the maxillæ. The base of the stylet is enlarged and triangular in shape (fig. 5). From the mesal edge of this enlarged base there extends to the maxillary sclerite in the head wall a crescent-shaped sclerite (fig. 5, *ca*). The dorsal edge of the piece is notched, and from the projection a tendon reaches to the tentorium (fig. 5, *mc*).

The musculature of the maxillæ is not complicated. There are two retractors (fig. 5, *mxr*), both of which reach from the inner surface of the epicranium to the base of the maxillæ. One protractor (fig. 5, *mxp*) fastens to the crescent-shaped sclerite, and the other to the lateral edge of the caudal face of the maxillary base. Both of these muscles are attached to the inner surface of the maxillary sclerite.

Upon removing the maxillæ, the heavier, outer pair of the stylets will be found directly beneath, as shown in the left side of figure 5. The mandibular base is at first apparently shaped like the maxillary base, but the dorsal part extends into two processes, one much wider and larger than the other. To the mesal one of these is attached the mandibular retractor (fig. 5, *mdr*). This muscle has a threefold origin; the strands unite, however, and fasten to the mandible by a single tendon. The

protractor muscle (fig. 5, *mdp*) extends from the cephalic face of the mandible to the maxillary sclerite (fig. 5, *mds*). It is a single muscle, but well developed. A quadrangular sclerite (fig. 5, *co*) serves to connect the mandible with the head wall. The joints are simple hinges, and the point of attachment is the dorsal end of the mandibular sclerite.

Figure 6 shows the enlarged tips of the stylets. The mandibles are serrated on the outer edges, but the maxillæ are smooth and sword-like. While in position the tips of the maxillæ are straight, but when free from the enclosing mandibles they assume a slightly recurved position.

The relation of the stylets to each other and the surrounding parts can best be studied by means of cross-sections. Figure 8 is such a section through the third labial segment. The stylets are all crescent-shaped, and through the central portion pass lumina (fig. 8, *l*), which are somewhat larger in the mandibles than in the maxillæ. The concavity of the mandibles is so great that they are almost able to enclose the small inner setæ. Although the maxillæ are side by side as they leave the head, by the time the third labial segment is reached, one is directly above the other. The inner surface of the upper maxilla is twice grooved. The three projections thus produced are mortised into the lower maxilla. This dovetailing is nicely done, and accounts for the difficulty in separating the two smaller setæ. It will be noticed that this device makes two tight tubes, one somewhat larger than the other. Around both sets of stylets is folded the strongly chitinized labium with its upper edges very closely appressed.

Passing from the third labial segment toward the head, there is little change in arrangement or structure until the first segment is reached. At this point the stylets enter the enclosing epipharynx (fig. 9). To this organ they are rather securely fastened by a grooved contrivance. A well-defined groove passes down each side of the upper part of the epipharynx and into these fit projections from the closely lying mandibles (fig. 9, *mg*). The maxillæ are not shown in the figure, but it can be readily seen how they are held between the concave mandibles. The epipharynx is itself in turn similarly attached to the labial wall (fig. 9, *lg*). This arrangement of interlocked parts explains why the organs at this point are separated with so much

difficulty. Where the stylets are held so tightly together by the encircling epipharynx, the mandibles and maxillæ rapidly diverge and enlarge into the basal portions already described. The position of the bristles in the head may be illustrated by a capital letter Y. The stem is made up of the four stylets and lies in the labium; the arms are each composed of a mandible and a maxilla, and one lies on either side of the head.

THE PHARYNX.

We are now ready to return to the brown, keel-shaped structure already mentioned as occupying the median portion of the head, and figured in the caudal views (fig. 4, *p*). This is the organ so frequently referred to by German writers as the "Schlundkopf." When dissected out it is only about 2 mm. long, and hence is best studied by means of cross- and longitudinal sections.

Figure 13 is a cross-section made through the upper edge of the clypeus. The form and position of the pharynx are at once apparent. It consists of two troughs (fig. 13, *p* and *pc*), one lying within the other. The lower one, a continuation of the mandibular sclerite, is much more strongly chitinized than the upper. Its inner surface is slightly grooved. Its outer convex surface is the part that meets our view in the caudal aspect. The upper fold, which is continuous with the frons and clypeus, is much more delicate than the lower, but toward the edges where the two folds coalesce, it is strongly chitinized and exceedingly elastic.

A slight thickening (fig. 14, upper *p*), which evidently serves for purposes of attachment, marks the median portion of the upper fold. Figure 12 makes the function of this part clear. Tendons are attached to the median part, and as they extend upward muscles branch off on either side pinnately. These muscles are fastened to the inner surface of the frons.

To obtain a more correct idea of the pharynx and its position in the head, a median longitudinal section will be most helpful. Figure 14 gives such a view. The organ under discussion is crescent-shaped, with one end facing the clypeus (fig. 14, *c*) almost squarely, and the other extending to the middle portion of the head. The caudal part is tubular, but slightly chitinized, and has all the appearances of the esophagus, into which it passes on its backward course. Cephalad

the lower part is strongly chitinized, and, in connection with the upper, more delicate fold, forms the double-trough-shaped portion already described (fig. 13). This trough-like structure, to continue the homely figure, terminates cephalad by the lower fold suddenly turning upward and forming a prow. From the base of the prow a strongly chitinized tube leads downward and backward, and terminates at the caudal extremity of the epipharynx.

THE HYPOPHARNYX.

In dissecting the head from the caudal side, a funnel-shaped, chitinized organ (fig. 3, *h*) is found at the lower end of the pharynx. This is the hypopharynx. The funnel shape is closely preserved only in the caudal portion, for in front the organ is fused with the pharynx. On each side of the latter the hypopharyngeal lamella extends dorsad, as a thin, chitinized plate (fig. 4, *cp*). These plates serve as a support for the large diverging muscles (fig. 3, *m.in*) already mentioned. The hypopharynx completely hides the tubular, canal part of the pharynx. On its caudal rim the hypopharynx ceases to be chitinous. From this point the tissue continues as a fleshy fold (fig. 14, *m*) until it passes into the dorsal surface of the labium, where it is again chitinized. The funnel tube sinks into the head and terminates in a tongue-shaped piece at the same point as the conduit from the pharynx. This is the part usually referred to as the true hypopharynx. The lower parts of the chitinous plates just mentioned, near where they fuse with the pharynx (fig. 13, *mg*), are fitted with the usual grooves and projections for holding and supporting the maxillæ. This structure corresponds to the far more elaborate "Fuhrungsleisten" described by German writers. In the *Cicada* they show nothing of the double fold and canal shape described by Geise for the Heteroptera.

THE SALIVARY INJECTOR.

Even in the coarse dissections with the needle, it appears that there is a chitinized organ lying in the cavity between the hypopharyngeal structures and the pharynx. The large converging muscles so prominent in the caudal view (fig. 3, *m.in*) meet at this point. But little more can be determined without the aid of cross- and longitudinal sections. For this organ I propose

the name of salivary injector. The reasons for the choice will appear as the discussion proceeds.

From sections we learn that the injector is a chitinized cylinder, furnished with a plunger, inlet and outlet tubes, and valves. An idea of its structure may be obtained from figure 14. One of the retractor muscles (fig. 14, *m.in*) is shown, although, correctly, it should not be figured in a median longitudinal section. The cylinder is conical at the cephalic end, compressed in the middle, and invaginated at the back. The central portion of the invagination is strongly chitinized, and serves as the point of attachment for a tendon which divides and sends a part to each of the large muscles of the injector (fig. 3, *m.in*). The rim of the cylinder is connected with the invaginated part by strong, elastic chitin. The normal position of the injector is that given in figure 14.

Among the Heteroptera Geise noticed, in regard to shape, two types of the injector. The water forms were all slightly spherical, while the land forms were cylindrical. A suggestion offered by him to account for the difference is, that the latter form gives greater elasticity, which might be required by the land form in forcing saliva into woody tissue. If this be true, we should expect to find the cylindrical form among the cicadas, and such is the case.

In the ventral side of the cylinder the entrance for a duct may be found. A valve (fig. 14, *v*) guards the opening, with the tip of its flap pointing toward the cephalic end of the cylinder. From this entranceway a single duct leads backward. As it leaves the encircling hypopharynx it divides, and in the caudal view (fig. 3, *sd*) these divisions may be easily traced. They lead back to the glands which fill the rear and upper part of the head chamber.

The cephalic portion of the cylinder narrows into a dark, heavily chitinized tube with which the hypopharynx is fused. Shortly beyond the point where the hypopharynx fuses, the tube coalesces with the pharyngeal canal, and the two pass forward as the tongue-shaped structure already mentioned in the discussion of the hypopharynx. The true nature of the structure may now be understood. It is the organ referred to by Savigny as ligula or hypopharynx. It is formed, first, by a fusion of the hypopharynx with the outlet of the injector; and,

second, by the fusion of these parts with the canal from the pharynx. The canals themselves remain distinct and terminate at the distal end in delicate processes.

At the point where the fusions take place a horny ring is formed, and this Gerstfeld makes mention of in the following words:

"Vorn am Kopfe, fast in gleicher Höhe mit der nach aussen daran liegenden Basen der Mandibeln und etwas uber denselben Theilen der Maxillen sieht man, wie es scheint, bei allen Hemipteren ein horniges oder lederartiges Stück ein wenig vorragen, welches nach dem Vorgange Savigny's von allen Naturforschern als Zunge oder Hypopharynx gedeutet worden ist. Es bildet den untern Theil des vordern Randes eines mehr oder weniger kurzen, hornigen Ringes, welcher den Anfang des Verdauungkanales röhrenformig umgiebt und tiefer in den Kopf hineindringt als die Mundtheile."

Gerstfeld and Burmeister both agreed in considering this part as an enlargement of the beginning of the alimentary canal rather than a fusion of the epi- and hypopharynx. They were correct in not referring its origin to a fusion of the epi- and hypopharynx, but only partly correct in their other conclusion, since they knew nothing of the salivary injector and its outlet. It is necessary that the pharyngeal and the salivary canals be kept distinct. At the same time, it is equally necessary that they be brought as closely as possible together. The point where they are first bound together shows a natural enlargement. Beyond this point the two tubes are thin and delicate, and extend forward until they are entirely surrounded by the encircling maxillary canals, which, it will be remembered, are made by the grooves in the concave side of the maxillæ. The horny ring, then, is not formed by the epi- and hypopharynx uniting to make the beginning of the tubular pharynx, but it is caused by a junction of the canals from the salivary injector and the pharynx.

PHYSIOLOGY OF THE PARTS.

Having described each organ in detail, we are now ready to discuss their functions. Before doing this, in order to get an idea of the parts as a whole, it is desirable to trace the lamellæ invaginated to form the mouth-parts from the exterior surface

through all of their modifications to the esophagus. Figure 14 will be useful for such a purpose.

The lamella composing the frons passes into the clypeus (*c*), and then bends back on itself, forming the short, triangular labrum (*l*). By bending a second time on itself, the longer, similarly shaped epipharynx (*e*) is formed, with its under surface well grooved to hold the stylets together. The lamella then differentiates into the upper part of the pharyngeal canal (*pc*), next into the upper part of the pharynx itself, and lastly into the esophagus. The lower lamella first outlines the labium (lab_3, lab_2, *lab*, and *la*). It then passes back as the membraneous portion (*m*) to the chitinized hypopharynx (*h*), which fuses with the walls of the salivary canal (*sc*). The walls of the cana' enlarge into the injector (*s.in*). From the dorsal wall of the salivary canal the lamella continues first as the lower portion of the pharyngeal canal (*pc*), next as the lower fold of the pharynx, and lastly as the esophagus.

The Hemiptera have always been known as sucking insects, but the problem has been to find out how the food reached the esophagus. From the descriptions of the parts, one must have already noticed that two of the organs have the character of pumps. Such is the case, the pharynx being an efficient suction-pump, while the salivary injector is a good force-pump. Perhaps the action and relation of all the parts may best be given by the imaginary feeding of some insect.

The tip of the beak is fitted with a tuft of hairs, a fact which is good evidence that the labium does not enter the body furnishing the food. Papillæ are present at the tip, and these serve as organs of touch and taste. The proboscis is held firmly against the bark, and, guided and supported by this encircling organ, the mandibles begin to bore, cut and saw their way into the cortex of the plant. The serrations at the tips of the mandibles (fig. 6, *md*) are especially fitted for this class of work. Within the mandibles ply the maxillæ, which are able to pierce deeply with their sword-like points. That this is the action of the stylets may be proved by the position of the protractor and retractor muscles, which are arranged to allow only such movements.

As soon as this action is established the salivary injector comes into play. The retractor muscles of the injector con-

tract and pull the chitinized piston back. The valve at the lower side of the chamber opens and saliva from adjoining reservoirs fills the cavity. As the muscle relaxes the elastic chitinous wall resumes its normal position, the valve closes, and the saliva is forced down the salivary canal into the smaller maxillary tube, through which it reaches the food supply. That this action is possible has been demonstrated by actual experiment. Although the injector is exceedingly small, under a suitable microscope I have succeeded in watching the movement of the elastic parts as the muscle of the injector was pulled back and forth mechanically. In some of the Heteroptera, Geise describes a valve for closing the salivary canal while the saliva is being pumped in from the glands. Wedde does not figure such a structure, and I am unable to find it in the *Cicada*. It is probable that at that point the canal is thin enough to press together and serve as a valve. In any case the efficiency of the injector would scarcely be affected, for the secretion might easily be forced into the chamber by the pressure of the reservoirs in which it is contained after having been secreted by the salivary glands.

The saliva of the Hemiptera is alkaline, and has the power of changing starch to sugar. Plateau made this discovery by boiling four of the glands from two *Nepas* in starch. Glucose was found in the mixture as a product. Primarily, then, the saliva serves as a digestive fluid. The fact that it is forced to the end of the labium, instead of being mixed with the food somewhere in the digestive tract, goes to show that the secretion has other uses. It is undoubtedly forced into the puncture made by the insect in order to increase the flow of sap. It also probably serves as a lubricant for the closely fitting maxillæ, since they would need something of the kind, and no other secretion is present.

As soon as a good flow of sap is started, the pharyngeal muscles (fig. 12, *m*, *p*) contract. By the alternate lowering and raising of the upper fold of the pharynx, a suction-pump is produced, the pipe for which is the pharyngeal canal and the upper maxillary tube into which the canal extends. The lower part of the tubes formed by the inner concave surfaces of the maxillæ are probably not air-tight. Suction, then, would not be sufficient to raise the fluid the entire distance from the tip

of the beak to the pharynx. It is, therefore, probable that capillarity accounts for the fluid rising in the lower part of the stylets. The action of the pharynx is, however, the stronger and more important of the two. There is no arrangement to prevent the fluid from flowing back when the pharyngeal muscles relax. Such a device would not be absolutely necessary, since the esophagus is the larger of the two tubes, and most of the food would pass that way. It is also possible for the muscles at the front to relax first, thus closing the pharyngeal canal and forcing the liquid into the esophagus.

Leon and Geise each figures serrations and papillæ on the inner surfaces of the pharynx. They suggest that these are used in grinding any granular food that the insect may take. The *Cicada* certainly has none of these devices, and it would seem that they were scarcely necessary in suctorial insects. The upper lamella of the pharynx is coarser where the pharyngeal tendons are attached, but this is due only to the natural enlargement of that portion.

A word here concerning the feeding habits of the cicadas may not be amiss. Early students of these insects held that the adults feed but little, if at all. Some have insisted that the females, needing nourishment for the process of egg-laying, take nourishment, while the males never do. In support of this view, it was announced that the digestive tract of the males was rudimentary. Marlatt, in his excellent report on the periodical cicada, makes the following statement:

"Such feeding is limited, at any rate, to the females, as in this sex only do we find a perfect digestive apparatus."

Until recently most of the suggestions on the subject were general and not supported by actual investigations. In June 1902, it was reported to Quaintance that the cicadas were feeding on an orchard near College Park, Maryland. His investigations give us the first authentic information on the subject. (Quaintance, 1902, *a* and *b*.)

Both males and females feed during the adult stage. Some of the beaks were snipped off by scissors and photographs then made of the parts. As described above, the tip of the proboscis was found resting on the bark while the stylets had pierced the cortex. Quaintance immediately dissected the digestive

tracts and found those of the males as well developed as those of the females.

In brief, then, the cicadas do not differ in their feeding habits from other Homoptera. Both males and females feed. If confined, they soon die from lack of nourishment. Occasionally orchards suffer severely from loss of sap given up as food.

MORPHOLOGY.

The morphology of the hemipterous mouth-parts still remains uncertain. Various interpretations have been presented, but the only ones on which investigators agree seem to be these: The parts are appendages of the head segments. The inner stylets correspond to the maxillæ, the outer to the mandibles. The sheath is made up of the labium and labrum.

No one attempted to work out the subject from an embryological point of view until Heymons. His results are valuable. At an early stage the appendages of all the head segments appear. The size of the clypeus is especially remarkable. The labrum appears late. The second maxillæ, which later fuse and form the labium, seem to have a tendency to fuse with the thorax. This fact accounts for the characteristic position of the beak in all Homoptera. The first maxillæ soon divide into a medial and a lateral lobe, termed the *lobus internus* and *lobus externus*. The medial lobe, termed the "Lade," together with the mandible, soon become retort-shaped, and later develop into the maxillary and mandibular setæ. The latter portion, the "Maxillenhocker," extends backwards and gives rise to the maxillary sclerite. The maxillary process appears early in the embryo. The top of the head is formed by large lateral lobes, the "Kopflappen." The sides of the head owe their origin mostly to the lateral maxillary lobe. The loræ or mandibular sclerites are related to the mandibles in mucb the same way as maxillary sclerites are to the maxillæ, but their origin is not made clear.

All of this knowledge is valuable, but it is not yet complete. Such questions as "What part of the typical maxillæ do the setæ represent, what has become of the maxillary and labial palpi, and what parts of the second maxillæ have fused to form the labium?" are yet unanswered. Embryological work, supplemented by the anatomical, will probably solve the problem.

With the exception of figures 1, 2, and 4, the drawings for this

paper were prepared by the author and inked in by Miss Margaret Wise. The figures mentioned were made from wash-drawings by Miss Wise. In conclusion, the writer desires to thank Prof. S. J. Hunter for his kindness and help. Without his interest and inspiration the work would have been a far more difficult undertaking.

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EXPLANATION OF ABBREVIATIONS

REFERRING TO PLATES VII TO XI.

at.....Anterior arm of the tentorium.
c.....Clypeus.
ca.....Crescent shaped sclerite attached to the maxillæ.
co.....Hinge connecting the mandible with the head wall.
cr.....Chitinous rod differentiated from the cephalic surface of the labium.
cp.....(In figs. 4 and 13.) Chitinized plate for the attachment of the muscles belonging to the salivary injector.
cp.....(In figs. 11 and 14.) The chitinized plunger in the salivary injector.
cm.....Muscles attached to the cervical sclerite for moving the head.
cmx.....Chitinized plates for attachment of the rotary muscles of the head.
csc.....Cervical sclerites.
e and *ep*....Epipharynx.
f.....Frons.
h.....Hypopharynx.
l.....Lumina.
la.....Labium.
lab (1 2 3)...First, second and third segments of labium.
lc.....Chitinized labial canal.
lp.....Labial protractor.
lr.....Labial retractor.
m.....Membrane connecting hypopharynx with labium.
mc.....Tendon connecting the crescent-shaped sclerite with tentorium.
md.....Mandible.
ml.....Muscles moving the entire head.
mr.....Rotary muscles of the head.
mg.....Process holding the maxillæ to the epipharynx and the chitinous plates.
mdp..... Mandibular protractor.
mdr.....Mandibular retractor.
min.....Muscles of the injector.
mds.....Mandibular sclerite.
mx.....Maxilla.
mxp.....Maxillary protractor.
mxr.....Maxillary retractor.
p.....Pharynx.
pc.....(In fig. 14.) The pharyngeal canal. In other figures, the lower lamella of the pharynx.
procx.....Maxillary process.
s.....Stylets.
sc.....Salivary canal.
sd.....Division of salivary duct.
sin.....Salivary injector.
t.....Tentorium.
tl.....Tip of labium.
tp.....Tendons of the pharyngeal muscles.
tmx.....Tip of maxilla.
v.....Valve in injector.
z.....Muscle for movement of head.

PLATE VII.

FIG. 1.—External cephalic aspect of the head.

FIG. 2.—Caudal view of the labium.

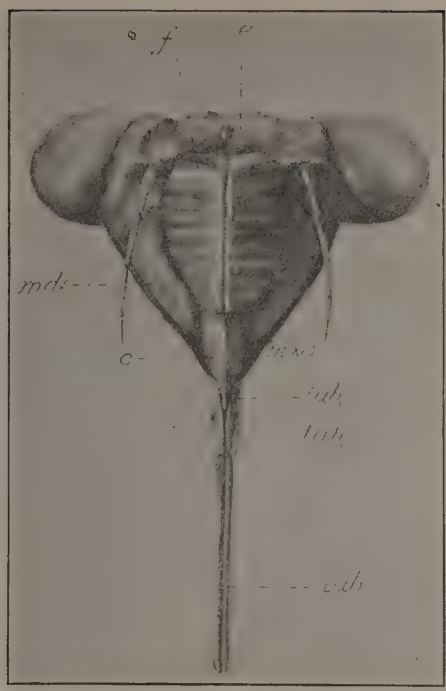


Fig. 1.

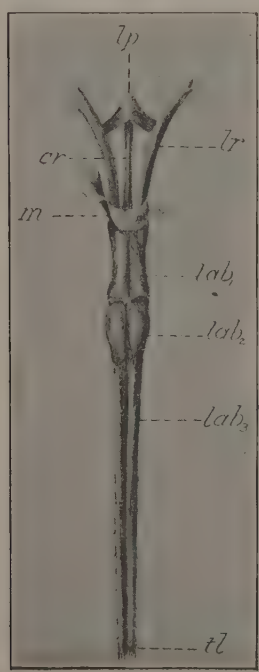


Fig. 2.

PLATE VIII.

Fig. 3.—Caudal view of the head as it appears when first removed from the body.

Fig. 4.—Caudal view of the head with the muscles removed to show chitinous structures.

Fig. 5.—Caudal view of the head with muscles and chitin removed to show the mandibles and maxillæ. A mandible with its attachments is shown on the left and a maxilla on the right.

Fig. 6.—Tips of mandibles and maxillæ.

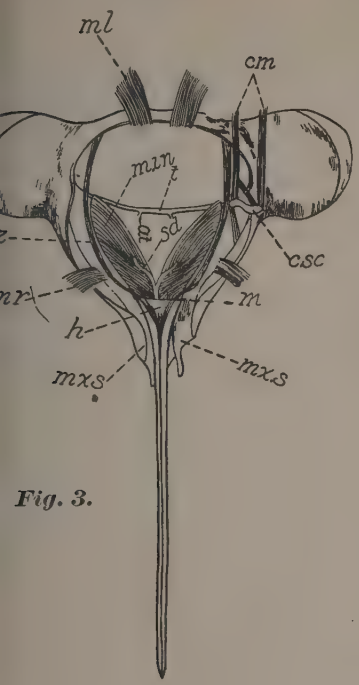
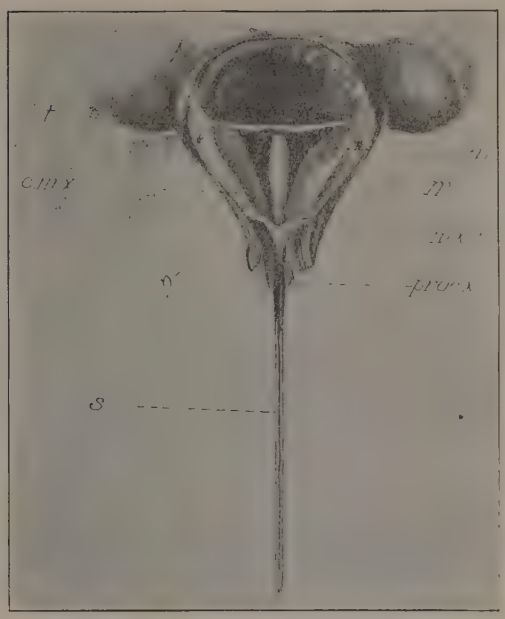


Fig. 3.

Fig. 4.



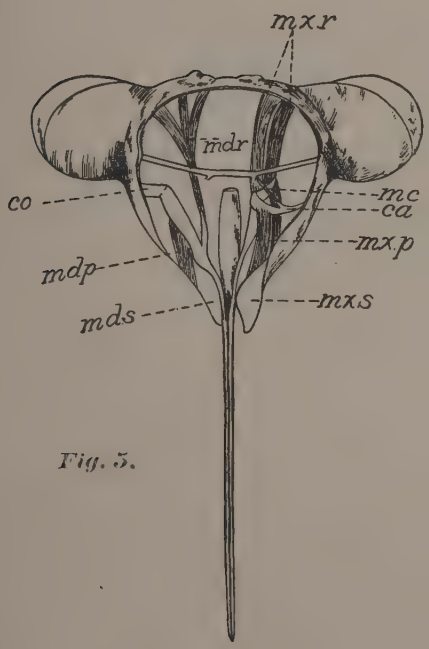


Fig. 5.

Fig. 6.

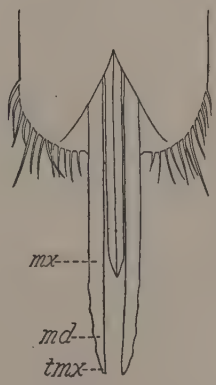


PLATE IX.

FIG. 7.—Under side of clypeus, showing closely lying structures.

FIG. 8.—Cross-section of labium. Third segment.

FIG. 9.—Cross-section through distal part of the clypeus.

FIG. 10.—Cross-section through proximal part of the clypeus.

PLATE IX.

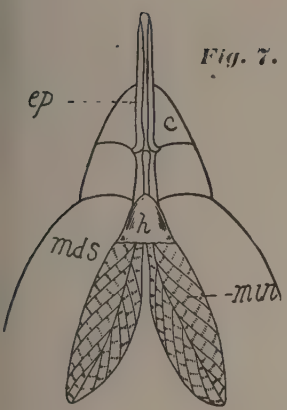


Fig. 7.

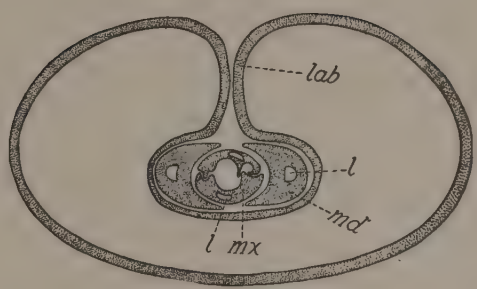


Fig. 8.

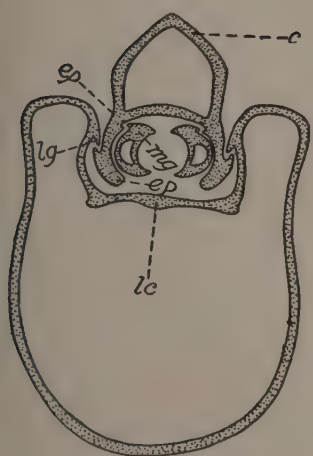


Fig. 9.

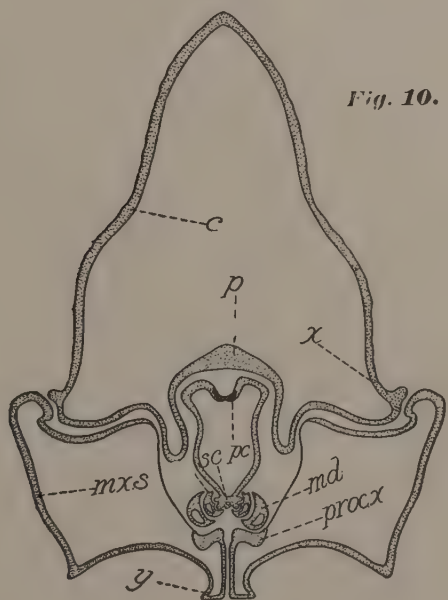


Fig. 10.

PLATE X.

Fig. 11.—Cross-section through the salivary injector.

Fig. 12.—Cross-section from epicranium to third labial segment.

PLATE X.

Fig. 11.

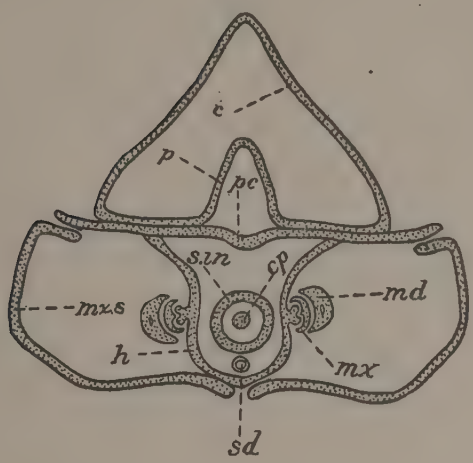


Fig. 12.

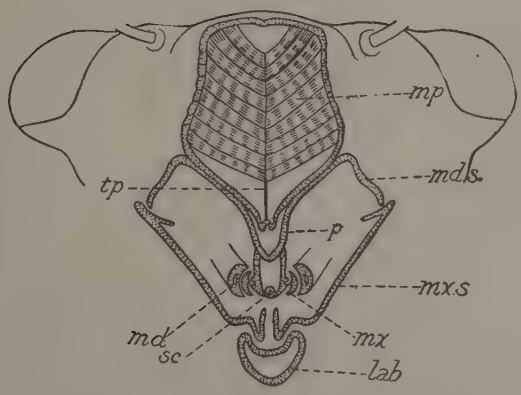


PLATE XI.

Fig. 13.—Cross-section through head caudad of the injector.
Fig. 14.—Median longitudinal section of entire head.

PLATE XI.

Fig. 13.

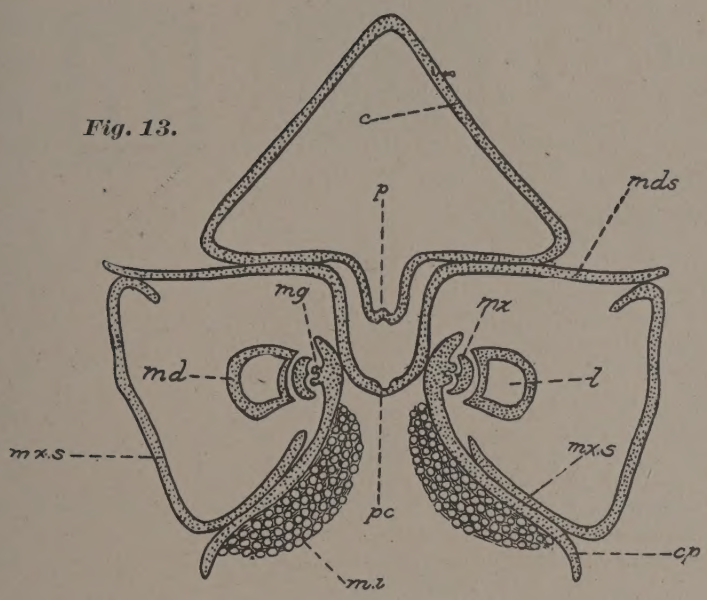
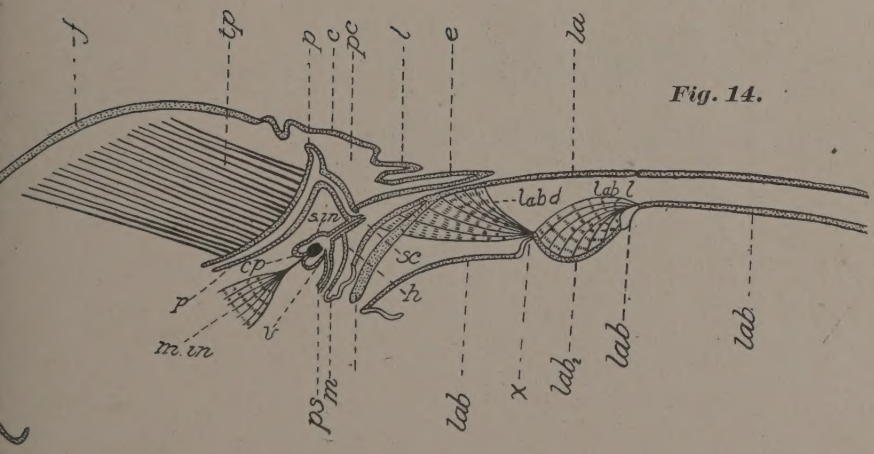



Fig. 14.